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ECOLOGICAL STRATEGIES AND IMPACT OF WILD BOAR IN PHYTOGEOGRAPHIC PROVINCES OF ARGENTINA WITH EMPHASIS ON ARIDLANDS

M. Fernanda Cuevas[1], Ricardo A. Ojeda[1] and Fabian M. Jaksic[2]

[1] Grupo de Investigaciones de la Biodiversidad (GiB), IADIZA, CCT Mendoza CONICET, CC 507, 5500 Mendoza, Argentina. [Correspondence: <fcuevas@mendoza-conicet.gob.ar>].
[2] Centro de Ecología Aplicada y Sustentabilidad (CAPES), Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

ABSTRACT. Wild boar is an invasive species introduced to Argentina for sport hunting purposes. Here, this species is present in at least 8 phytogeographic provinces but we only have information in four of them (Pampean grassland, Espinal, Subantarctic and Monte Desert). We review the ecological strategies and impact of wild boar on ecosystem processes in these different phytogeographic provinces and identify knowledge gaps and research priorities for a better understanding of this invasive species in Argentina. We observe that foraging strategies of wild boar consist in consuming mainly plant species rich in energy, especially those with bulbs and fuits having high concentrations of carbohydrates and lipids, and the use of habitat is closely associated with food resource availability. Wild boar generate a broad variety of impacts reflected in plant species composition, structure and biomass, and changes in soil properties such as increased soil degradation in the Monte Desert. We conclude that the impacts of wild boar in Argentina are mostly negative, demanding more interaction among relevant players (scientists, government officials, managers of protected areas, and landowners) to plan the population control strategies needed to mitigate damage to native ecosystems and agricultural production in the country.

RESUMEN. Estrategias ecológicas e impacto del jabalí en provincias fitogeográficas de Argentina con énfasis en las tierras áridas. El jabalí es una especie exótica introducida en Argentina para la caza deportiva. Aquí, esta especie está presente en al menos 8 provincias fitogeográficas aunque solo tenemos información para cuatro de ellas (Pampeana, Espinal, Subantártica y Desierto del Monte). Se hace una revisión de las estrategias ecológicas y del impacto del jabalí sobre el ecosistema invadido en diferentes provincias fitogeográficas de Argentina, identificando los vacíos y necesidades de investigación para un mejor entendimiento de esta especie invasora. Observamos que la estrategia de forrajeo del jabalí consiste en consumir principalmente especies de plantas ricas en energía, con un alto contenido de carbohidratos y lípidos presentes en bulbos y frutos; y que el uso del hábitat está principalmente asociado con la disponibilidad de los recursos alimenticios. El jabalí en Argentina genera una amplia variedad de efectos relacionados con la composición, estructura y biomasa de la vegetación, y con cambios en las propiedades del suelo, donde genera un aumento de la degradación del mismo, ejemplificado en el Desierto del Monte. Concluimos que el impacto generado por el jabalí en Argentina es mayormente negativo, por lo que es necesaria la interacción de diferentes actores (científicos, gobierno, administradores de

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áreas protegidas y propietarios de campos) para planificar una estrategia de gestión y control de las poblaciones de jabalí, y por lo tanto mitigar su daño sobre el ecosistema nativo y los sistemas productivos del país.

Key words: Argentina. Disturbance. Foraging. Habitat. *Sus scrofa.*

Palabras clave: Argentina. Disturbios. Forrajeo. Hábitat. *Sus scrofa.*

INTRODUCTION

The wild boar (*Sus scrofa*) is native to Eurasia and northern Africa (Long, 2003), but now has one of the widest geographic distributions of all exotic mammals (Oliver et al., 1993). Due to the damage it causes in natural ecosystems and agricultural areas, it is considered one of the 100 most harmful invasive species of the world (Lowe et al., 2000). The wild boar is an omnivorous species with a diet dominated by plant material (between 87 and 99%) and a smaller representation of animal matter (Schley and Roper, 2003). It has a high reproductive capacity due to characteristics such as precocious sexual maturation (from 5 to 12 months), its relatively short gestation time (120 days), and large litter size (5-7 piglets) (Gethöffer et al., 2007; Herrero et al., 2008). It also has a high tolerance to different climatic conditions, reflected in its wide geographic range (Oliver et al., 1993). For all these traits, wild boar has expanded successfully to all continents except Antarctica (Long, 2003). Nowadays this species occurs in different parts of the world either in pure wild or barely-modified feral form due to its crossing with domestic pigs (Baber and Coblentz, 1986; Merino and Carpinetti, 2003).

In its native range, this species occupies different types of habitats such as forests, shrublands, mangroves, grasslands, and wetlands (Rosell et al., 2001). In spite of that, wild boar prefers those habitats that offer high energy food, such as acorns, and have high vegetation cover for protection from predators (including hunters), as well as those close to water resources (Kurz and Marchinton, 1972; Massei and Genov, 1995).

Several climatic and ecological factors have been described to affect the abundance and distribution of wild boar (Jedrzejewska et al., 1997; Acevedo et al., 2006). For example, rainfall generates an increase in the number of pregnant females during rainy years (Fernández-Llario and Mateos-Quesada, 2005). Hunting pressure also affects its spatial behavior by modifying choice of resting sites (Scillitani et al., 2009). Heterogeneous landscapes (i.e., high diversity of food resources and high availability of shelters) also favor high densities of wild boar as compared to homogeneous habitats (Fernández-Llario, 2004; Acevedo et al., 2006).

The wild boar is considered an ecosystem engineer due to its rooting behavior, which transforms the physical state of biotic and abiotic materials (Jones et al., 1994; Crooks, 2002). To forage, wild boars overturn extensive areas of soil, leaving them bare of vegetation (Hone, 1988). This rooting behavior creates a complex mosaic of disturbed patches of different ages and sizes (Cuevas et al., 2012). This type of activity sometimes generates benefits to native and exotic flora, such as increasing plant richness and cover of perennial grasses (Tierney and Cushman, 2006). But it also causes negative effects such as mixing soil horizons, reducing vegetative cover and litter, accelerating the leaching of ions from litter and soil (e.g., Ca, P, Zn, Cu, and Mg), increasing nitrate concentrations and soil respiration, and decreasing the abundance of soil arthropods (Singer et al., 1984; Mohr et al., 2005; Risch et al., 2010).

Here we review and summarize the literature on wild boar ecology and ecosystem impacts in different phytogeographic provinces of Argentina, identifying knowledge gaps and research priorities toward a better understanding of this invasive species in Argentina. The aims of our contribution involve an overview of scientific studies of wild boar ecology and impact in Argentina, with a particular focus in their ecological strategies to survive in semi-arid conditions.

We performed searches in specialized journals and data bases (e.g. Blackwell, Elsevier, Google Scholar, Scielo and Scopus), using different combinations of the following keywords: *Sus scrofa*, feral pig, wild boar, ecology, feeding habits, diet, habitat use, impact, Argentina. We also reviewed doctoral and Master's theses. We set the search for studies between 1970 and 2015 and included studies referring to wild boar and feral pigs. The literature search yielded 234 studies of which 17 were relevant to the objective of this study (**Table 1**), from which we found 13 scientific articles, 3 doctoral theses and 1 technical report related to wild boar ecological strategies (i.e., way in which the species uses available resources in the invaded habitat, such as diet, habitat use, resource selection, that permit wild boar to survive in it) and impact on soil properties and plant species composition and structure.

THE WILD BOAR IN ARGENTINA

The wild boar was first introduced to Argentina in 1906 in San Huberto ranch, La Pampa for hunting purposes (Daciuk, 1978). After that, wild boar reintroductions occurred several times in different parts of the country, such as in Collun-có ranch, Neuquén in 1917 and Huemul ranch, Río Negro in 1924 (Daciuk, 1978). Furthermore, the continuous installation of hunting grounds involves the introduction of new populations of this species around the

Table 1

Summary of wild boar studies in the phytogeographic provinces of Argentina.

Phytogeographic province	Impact	Ecological traits	References
Pampean grassland	Potential impact on Pampas deer (*Ozotoceros bezoarticus celer*) populations	Population abundance	Merino and Carpinetti (2003); Perez Carusi et al. (2009)
Espinal	Seed predation of *Butia yatay*	Diet, habitat use	Govetto (1999); Ballari (2013); Ballari et al. (2015b)
		Habitat use, distribution range expansion	Schiaffini and Vila (2012); Gantchoff and Belant (2015); Pescador et al. (2009)
Subantarctic	Impact on vegetation and soil properties		Barrios-García (2012); Barrios-García and Simberloff (2013); Barrios-García et al. (2014)
	Seed predation of *Araucaria araucana*		Sanguinetti and Kitsberger (2010)
Monte Desert	Impact on vegetation and soil properties		Cuevas et al. (2010); Cuevas (2012); Cuevas et al. (2012)
		Diet, habitat use	Cuevas et al. (2013a); Cuevas et al. (2013b)

country. In a recent study, Ballari et al. (2015a) evaluated the current status of wild boar in Argentina's system of protected areas. They showed that wild boars are present in at least 10 ecoregions belonging to 8 phytogeographic provinces (High Andean, Monte Desert, Chaco, Paranaense, Pampean grassland, Espinal, Patagonian and Subantarctic provinces) (**Fig. 1**). While in the rest of the provinces (Puna, Prepuna, Yungas) they did not find any record of this species. They also found novel ecoregions being occupied by this species, like High Andean, Parana Flooded Savanna and Iberá Marshes, which indicates that wild boars are continuously expanding their geographic range in Argentina. Nevertheless, studies about their ecology and ecosystem impacts in different biomes of Argentina are scarce. Information is available in only four phytogeogeographic provinces: Pampean grassland, Espinal, Subantarctic region, and Monte Desert (**Fig. 1**, **Table 1**).

Pampean grassland

The climate of this province ranges from temperate to warm, having rainfall throughout the whole year that decreases from north to south and from east to west (range: 600-1100 mm rainfall annually). Dominant vegetation is grasslands with a lower presence of halophyte steppes, marginal forests, and several types of hydrophilic shrubs (Cabrera, 1971).

For this biome, there are two studies about *Sus scrofa*, in which area occur feral populations of domestic pigs, both in Bahía Samborombón (35°26' S, 57°47' W) where feral pigs were reported in 1980 (Merino and Carpinetti, 2003; Pérez-Carusi et al., 2009; Ballari et al., 2015a) (**Table 1**). This area has an annual precipitation of 1000 mm and small patches of "tala" forest (*Celtis tala*) surrounded by humid and salty grasslands (Cabrera, 1971). This area has a special significance as a refuge for several native species that have disappeared in other parts of the Pampas region (Merino and Carpinetti, 2003). Between 1995 and 1998, Merino and Carpinetti (2003) assessed feral pig populations using aerial counts. They found that pig abundances showed an accelerated increase, from about 700 individuals at the beginning of the study to more than 2000 at the end, including several peaks reaching over 4000 individuals.

A second study conducted by Perez Carusi et al. (2009) used the same methodology of counting, but also compared the spatial distribution and abundance of feral pigs with the sympatric pampas deer (*Ozotoceros bezoarticus celer*), a native species with endangered conservation status (Ojeda et al., 2012). They reported indirect evidence of a potential negative impact of feral pigs on pampas deer: compared to previous years there was a decrease in pampas deer abundance and spatial distribution while feral pigs increased on both counts. The authors also suggested that the decrease in abundance of pampas deer could be related to other factors such as the outbreak of FMD (foot and mouth disease) and/or the effect of poaching. Still, Perez Carusi et al. (2009) found a negative correlation between abundances of pampas deer and feral pigs, but did not assess the habitat or food use of these two species. Although pampas deer is a strict herbivore and pigs are omnivorous, the bulk of feral pig diet is plant matter (90%) (Schley and Roper, 2003; Ballari and Barrios-García, 2014). Further research on the niche axes (e.g., food, habitat) of these species may provide a more thorough assessment of their coexistence mechanisms.

Pérez Carusi et al. (2009) observed a 400% increase of pig population during the period of study. However, this finding should be taken cautiously, because at the end of Merino and Carpinetti's (2003) study, pig population was over 2600 individuals, while in Pérez Carusi et al.' (2009) study it was 2690 individuals. Still, comparing both studies, there was a substantial increase in pig density, from 1.59 ind/km^2 to 7.78 ind/km^2. It should be noted that these studies differed in number of sighting trips and transects, and the size of surveyed area.

Espinal

The Espinal phytogeographic province has a diverse climate that changes latitudinally from warm and wet in the northern part to temperate and dry in the central and southern areas.

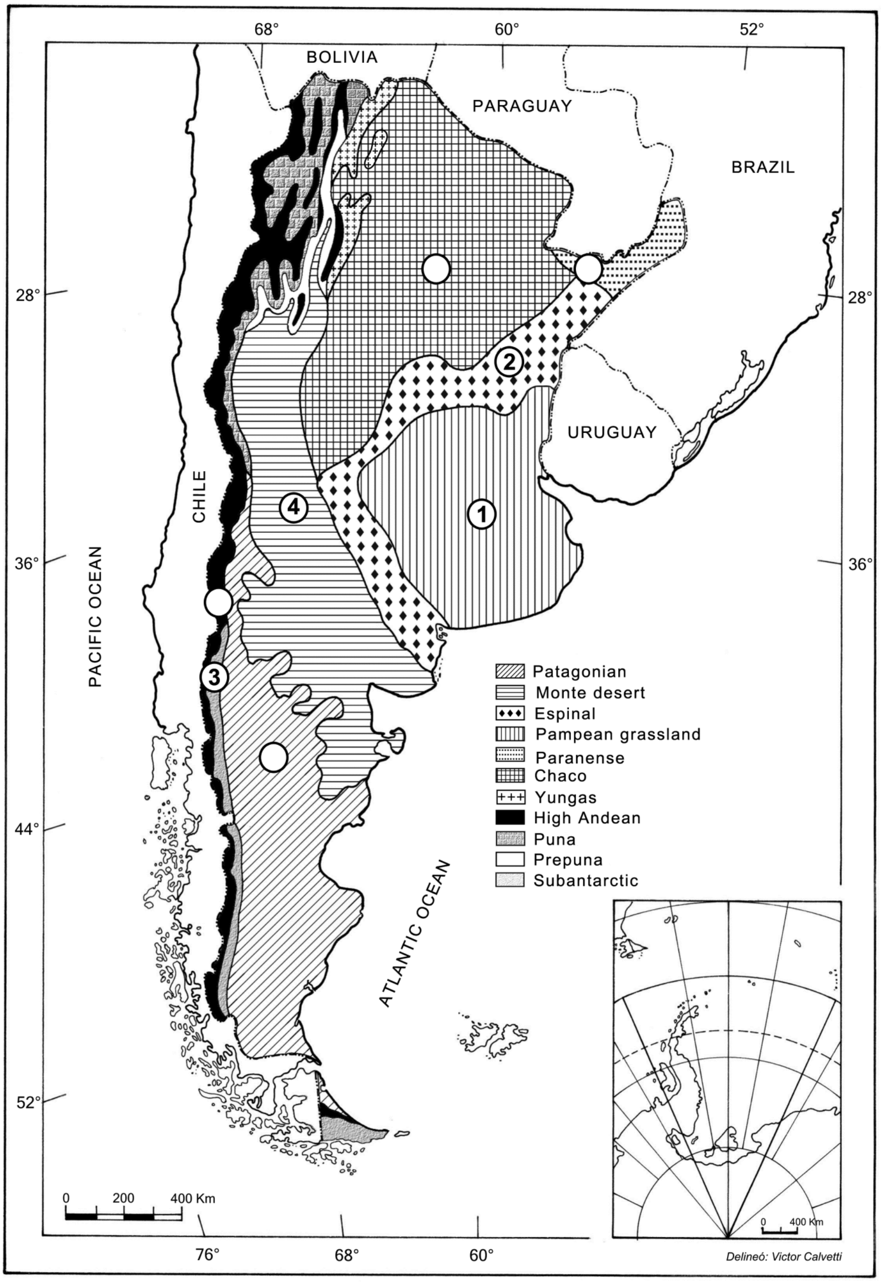

Fig. 1. Argentine phytogeographic provinces showing the presence of wild boar (white circles). Numbers indicate provinces with ecological and ecosystem impact information of the species. Map extracted from Katinas et al., 2007.

Accordingly, the vegetation also varies, showing deciduous dry forests, palm groves, grasslands, savannahs and shrub steppes (Cabrera, 1971).

The southern part of this region was home to the first introduction of wild boar in Argentina (San Huberto ranch, La Pampa province). Despite having the oldest wild boar population in the country, there is no scientific information evaluating its interactions with native species or the impact upon the invaded ecosystem. Instead, the ecology and impacts of wild boar in this region have been conducted in an area that differs markedly from the introduction site: El Palmar National Park (EPNP), Entre Rios province (31°50' S, 58°17' W) (Govetto, 1999; Ballari, 2013; Ballari et al., 2015b) (**Table 1**). The landscape is characterized by a heterogeneous mosaic of vegetation patches that includes gallery forests, shrublands, grasslands and savannahs, with Yatay palms (*Butia yatay*) in highlands (Movia and Menvielle, 1994). The climate is warm (annual mean temperature 28.9 °C) and wet throughout the year with no dry season (annual mean precipitation 1300 mm; Papadakis, 1974). Wild boars have been reported in this protected area since 1950 (Ballari et al., 2015a).

Based on stomach contents, Ballari et al. (2015b) found that 81.2% of the wild boar diet at EPNP is plant material and almost 18.8% is animal matter. They observed that during the fruiting of Yatay palm (an endemic and protected species) wild boars eat those fruits to reach approximately 50% of their diet in summer. But during winter/autumn and spring, when those fruits are not available on the ground, boar fed mainly on corn (a supplemental feeding used in EPNP for controlling the species, and to promote hunting), this item comprising between 40 and 50% of the diet. Only during spring, the bulk of the diet is corn (42%) and animal matter (27%). So, it appears that during the masting period of Yatay palm, boars prefer to eat it over the supplemental corn. The relatively high dietary content of animal matter in EPNP could be related with the ingestion of corn and fruits of *Butia* spp., whose species are high in carbohydrates but low in protein (Schley and Roper, 2003; Hoffman et al., 2014). So their gain of caloric requirement from corn may cause wild boar to compensate for lack of protein by eating more animal matter (Schley and Roper, 2003).

Regarding habitat use, Govetto (1999) found a high density of wild boar signs in Yatay palm forest during the masting period (February and March), and also Ballari (2013) found that wild boar prefers habitats with a dominant tree canopy, e.g., Yatay palm forest and forest of exotic xerophytes (white cedar *Melia azedarach*, Gigg's firethorn *Pyracantha atalantoides*, honey locust *Gleditsia triacanthos*, broad-leaf privet *Ligustrum lucidum*, Chinese privet *Ligustrum sinense*). Agricultural lands that surround the park were not preferred by wild boars, possibly due to abundant food resources present in the park, including the supplemental feeding (corn) for hunting practices (Ballari et al., 2015b).

Subantarctic

The climate of this phytogeographic region is temperate and wet with mean temperature 9.5 °C in the northern portion and 5.4 °C in the south. Annual precipitation goes from 2000 mm on the west bordering with Chile to 750 mm to the east of this region. Dominant vegetation types are pure or mixed forests of conifers like cordilleran cypress (*Austrocedrus chilensis*, Fam. Cupressaceae) and alerce (*Fitzroya cupressoides*, Fam. Cupressaceae), evergreen species like coihue (*Nothofagus dombeyi*, Fam. Nothofagaceae), and deciduous species of southern beech such as ñire (*N. antarctica*, Fam. Nothofagaceae) and lenga (*N. pumilio*, Fam. Nothofagaceae). These forests are mixed to a lesser extent with grasslands and peatlands (Cabrera, 1971). Wild boars have been introduced to Patagonian forest since 1917 (Daciuk, 1978).

Within this region, wild boar studies have focused on habitat use, distribution range and impact on soil properties and vegetation (Pescador et al., 2009; Sanguinetti and Kitsberger, 2010; Schiaffini and Vila, 2012; Barrios-García, 2012; Barrios-García and Simberloff, 2013; Barrios-García et al., 2014; Gantchoff and Belant, 2015) (**Table 1**).

Regarding habitat use, Schiaffini and Vila (2012) registered the presence of wild boar signs through transects along an altitudinal gradient (from 300 to 1200 m elevation) at

Los Alerces National Park (LANP, 42°50' S, 71°52' W). They found that between 600 and 700 m there was the highest abundance of wild boar signs and that at elevation 1200 m there was no evidence of its presence. *Nothofagus dombeyi* and *N. antarctica* forests were used by this species more than forests of *N. pumilio* and grasslands. The authors concluded that the increased presence of wild boar in intermediate elevations was associated with the dense understory vegetation of *Nothofagus* forests, which provides warmth and moisture conditions that boars need to meet thermal requirements. Also, the high canopy (40 m) provides shelter from hot summer temperatures (~30 °C). Further, the dense understory of bamboo (*Chusquea culeou*) affords protection from frost during cold days, allowing boars to find food under it.

Gantchoff and Belant (2015) evaluated the influence of environmental and anthropogenic factors on wild boar occurrence in a tourist site of Nahuel Huapi National Park (NHNP, 40°57' S, 71°33' W) using camera traps. Similarly as in Schiaffini and Vila's (2012) study, they found that wild boar frequently uses *Nothofagus dombeyi* and *N. antarctica* forests compared with *N. pumilio* forests. They found that longer distance to human settlements and closer distances to roads were the most important anthropogenic variables influencing the occurrence of wild boar in the park. That result plus the boars' nocturnal activity indicates that boars use roads as corridors to move across forests while avoiding human due to hunting pressure (Gantchoff and Belant, 2015).

Regarding distribution range, Pescador et al. (2009) assessed the presence and the relative abundance of wild boar in 1985 and then repeated it in 2005 along transects in Lanín National Park (LNP, 39°34'S, 71°27'W). They found that after 20 years wild boar increased its range with a spread rate of 3500 ha per year.

Studies about impact of wild boar on vegetation structure, seed predation, and soil properties were recently conducted in LNP and NHNP. At NHNP, Barrios-García et al. (2014) studied the impact of wild boar on vegetation and soil properties through an enclosure experiment in three different plant communities: *Austrocedrus chilensis*, *Nothofagus dombeyi* and shrublands. Results showed that wild boar rooting generates a 60% reduction in aerial plant biomass, this negative effect being stronger in *Nothofagus* forests. Cover of herbs and grasses was lower in rooting patches, herb cover being least in *Austrocedrus* and *Nothofagus* forests while grass cover was also lower in *Nothofagus* forest. Shrub cover was also negatively affected by rooting, but it was in shrubland that the authors noticed the major impact. Regarding litter decomposition rate, this was lower in rooting patches. At soil level, wild boar rooting only modified soil compaction, making this attribute lower in both forests (**Table 2**). Finally, the authors concluded that impact caused by wild boar is greater aboveground than belowground.

In a second enclosure experiment Barrios-García and Simberloff (2013) evaluated the effect of rooting on non-native seedling establishment and plant growth, and wild boar's role in seed dispersal of native and exotic plant species. Rooting patches showed higher non-native seedlings and biomass of seedlings, biomass being greatest in shrublands. All exotic plant species except for sweet brier (*Rosa rubiginosa*) and elmleaf blackberry (*Rubus ulmifolius*) showed higher establishment in rooting patches. The authors also found that both soil samples and feces showed equal composition of seed species, but in fecal samples there were fewer non-native species of seed compared with soil samples. Lastly, they found a positive effect (invasional meltdown) in the establishment of non-native seedlings in rooting patches and a negative effect in non-native seed dispersal.

Sanguinetti and Kitzberger (2010) evaluated the impact of wild boar on seed survival and seedling establishment of *Araucaria araucana* in LNP through an experiment at different distances from a female tree of araucaria. The authors observed that wild boars preferred mixed *A. araucaria–N. pumilio* over *A. araucaria–N. antarctica* forests for feeding. They found that wild boar consumed between 10 and 30% of available seeds. Predation was greater in places with low plant cover and close to seeding trees. When they excluded wild boars, they found that the number of surviving seeds increased, resulting in higher seedling establishment during non-masting years (boars

Table 2

Effects of wild boar's rooting in soil properties in both Monte Desert and Subantarctic phytogeographic provinces.

Soil Properties		Monte Desert		Subantarctic Forest	
		Disturbed	Undisturbed	Disturbed	Undisturbed
Physical	Hardness	–	+	–	+
	Moisture	+	–	No change	
	Temperature	--------	--------	No change	
	Texture				
	Silt	–	+	--------	
	Clay	–	+	--------	
	Sand	+	–	--------	
Chemical	Total Nitrogen	No change		No change	
	Mineral Nitrogen	+	–	No change	
	Nitrate + Nitrite	+	–	--------	
	NH_4	No change		--------	
	Organic Carbon	No change		--------	
	C/N ratio	+	–	--------	
	Organic matter	No change		--------	
	pH	No change		No change	
	Total Carbon	--------		No change	
	Extractable P	--------		No change	
Microbiological	Soil respiration	–	+	No change	
	Ammonifiers	No change		--------	
	Cellulolytics	No change		--------	
	N fixers	No change		--------	
	Nitrifiers	No change		--------	

ate proportionally more seeds during such periods than during masting). Finally, the negative effect of wild boar was reflected at individual tree level, but not at population scale.

To sum up, wild boars in the Subantarctic region more often use *Nothofagus* forests and those habitats are the most affected by rooting behavior. The disturbance by wild boar affects properties not only at community level but also at ecosystem scale, changing plant community composition and structure, decreasing decomposition rates, and promoting invasive plant establishment and growth.

Monte Desert

Aridlands are one of the most extensive terrestrial habitats on the planet, occupying about a third of the Earth's surface. Aridlands are characterized by high temperatures, water deficit and low plant productivity, generating a great challenge to the survival of plants and animals in these environments (Cloudsley-Thompson, 1975; Brown et al., 1979; Polis, 1995).

South American aridlands have played an important role in the evolution of the temperate biota of the continent, with high biological diversity that contains a large percentage of endemic genera and families (Ojeda et al., 1998). In Argentina, aridlands are undergoing rapid habitat conversion as a result of human activities (agriculture, grazing, logging, etc.), desertification, and salinization (Ojeda and Mares, 1982). To these challenges, environmental changes driven by climate change are added, as well as changes caused by invasive species (Boulanger et al., 2007; Cuevas et al., 2012). Considering that the temperate biomes of Argentina concentrate the highest numbers of invasive mammals of South America (Ojeda et al., unpublished data), the study of invasive species in the process of expansion is an interesting opportunity to assess the conditions and constraints that these species face within the dynamics of aridland invasibility.

In Argentina, 57% of the territory consists of aridlands (Verbistk et al., 2010). Overall, there are 23 exotic species of mammals (including feral populations of domestic species), with at least six of them found in this region: wild boar (*Sus scrofa)*, European rabbit (*Oryctolagus cuniculus*), European hare (*Lepus europaeus*), blackbuck (*Antilope cervicapra*), donkey (*Equus asinus*), red deer (*Cervus elaphus*) (Novillo and Ojeda, 2008).

Monte Desert is a subtropical to warm temperate desert and semidesert located in western Argentina (Abraham et al., 2009) (**Fig. 1**). The climate is dry and warm in the northern portion and dry and cold in southern part of this phytogeographic province. The precipitation varies between 80 and 250 annual mm, and temperature from 48°C to -17°C (Labraga and Villalba, 2009). Dominant vegetation types are shrubland steppes of xerophytes, psammophytes or halophytes, as well as marginal *Prosopis* woodlands (Cabrera, 1971).

In this region, wild boar has been studied from a great variety of aspects, including habitat use, diet, climatic influence, and impacts on vegetation composition and on physical, chemical and microbiological soil properties (Campos and Ojeda, 1997; Cuevas et al., 2010; Cuevas, 2012; Cuevas et al., 2012; Cuevas et al., 2013a; 2013b) (**Table 1**). Although wild boar is not physiologically adapted to arid environments (Baber and Coblentz, 1986), they have successfully colonized them worldwide, such as in the deserts of USA, Australia, and Argentina (Barrett, 1978; Saunders and Giles, 1995; Cuevas et al., 2010). For that reason, studies that help us understand the ecological strategies that boars use in environments quite different from their native range may yield insights about the traits and factors that constraint or facilitate the expansion of invasive species.

Wild boar studies within this phytogeographic region have been conducted in the Man and Biosphere (MaB) Reserve of Ñacuñán (34°02′ S, 67°58′ W), Mendoza province. The landscape is characterized by a heterogeneous mosaic of vegetation patches. Dominant habitats are *Prosopis* woodland or algarrobal (*Prosopis flexuosa*, Fam. Fabaceae), *Larrea* shrubland or jarillal (*Larrea cuneifolia*, Fam. Zygophyllaceae), and sand dunes. The climate is semiarid and strongly seasonal, with hot, humid summers and cold, dry winters. Mean annual precipitation and temperature are 326 mm and 15.6 ºC, respectively, with a maximum annual mean of 23.8 ºC and a minimum annual mean of 7.6 ºC (Estrella et al., 2001; Labraga and Villalba, 2009). Wild boar was first sighted in this area in the 1980's (Cuevas et al., 2010).

Cuevas et al. (2013a) studied habitat use by wild boar through signs such as tracks and rooting. Considering tracks at the habitat level, the authors did not find any difference among the three available habitats, which means that at least for displacement (moving from one place to another) wild boars used the different habitats in proportion to their availability. Regarding rooting activity they found that wild boar positively selected *Larrea* shrubland and avoided *Prosopis* woodland. At the microhabitat level, herb cover was the most important factor affecting wild boar presence, showing a positive association between this and the abundance of signs.

Based on wild boar feces, Cuevas et al. (2013b) found that the diet consisted of 96% plant matter and 4% of animal matter. Herbs were the most frequently consumed food item (~50%) followed by woody species. Aerial parts were consumed more frequently during the dry season, whereas during the wet season, fruits and animal tissue were more frequent. Regarding trophic selection, herbs were the only food item selected by wild boars, while trees like algarrobo dulce (*Prosopis fleuxosa*) were consumed as available only during the wet season, which is the season where this tree species bears fruit. They also found that wild boar used food resources according to seasonal availability, observing a broader trophic niche with higher plant diversity in the wet season. Finally, the most consumed food items (fruits of *Prosopis flexuosa*, leaves of malvisco [*Sphaeralcea miniata*], and bulbs of papilla [*Pitraea cuneato-ovata*]) had high forage quality and high carbohydrate contents, which means immediate energy for the organism.

Cuevas et al. (2013a) found that wild boars used the habitat as a function of food availability. This is because *Larrea* shubland, which was the only habitat selected by boars through rooting sign (their main way of finding food), is associated with high herb cover, and herbaceous plants were the most frequent food item as well as preferred in their diet (Cuevas et al., 2010; Cuevas et al., 2013b). High carbohydrate input is considered important in the diet of an individual as it is an essential component in keeping the body in good physical condition and also for the accumulation of reserves to be used during more critical periods (food scarcity) and/or periods of highest energy demand (reproduction) (Abaigar, 1993). Furthermore, around this protected area there are no croplands so the ingestion of energy-rich food is crucial for boar survival, particularly in arid conditions where the majority of plants have high fiber content and low nutritional value (Noy-Meir, 1973). This foraging strategy enables wild boar to maximize energy budget through food selection. Besides being a generalist species (Rosell et al., 2001), in the semiarid environment of the Monte Desert the wild boar appears as a species that selects both space (habitat use) and food (herbs) (Cuevas et al., 2013a; 2013b).

Regarding climatic influences on wild boar activity at local scales, Cuevas et al. (2013a) found a positive association between the number of days with low temperature and the number of wild boar signs recorded in the Reserve. This means that the seasonal activity and/or daily movements of wild boars in periods or seasons of high temperature were reduced. Thus, temperature could be a limiting factor for wild boar activity, especially in aridlands, because boars lack sweat glands or other cooling physiological mechanisms for maintaining hydric and thermal balance. They require free water, shade, a diet rich in water, and/or a behavioral response to increased environmental temperatures (Rosell et al., 2001; Dexter, 2003). In the Monte Desert, Cuevas et al. (2013a) found that wild boars showed a behavioral response related with daily movements patterns to increased environmental temperature, but they did not find a strong association with free water.

To sum up, ecological strategies of wild boar in aridlands of Argentina where water resource is scarce and exposure to sun is high, shade could be essential for surviving. Therefore, it is necessary that wild boars minimize the exposure to high temperatures and maximize the food intake of high quality forage to maximize their energy input.

According to Campos and Ojeda (1997), wild boar causes damages by chewing nearly 100% of ingested seeds of *Prosopis flexuosa*. While that study was based on only 3 samples of feces, a more recent study (Cuevas, unpublished data) has observed that of a total of 1618 seeds (39 fecal samples), 30% had the entire (apparently healthy) seed coat while the remainder 70% was damaged, either by boar chewing (17.3%), bruchid insects (31.7%), or other causes (21%). Nevertheless, of all the "healthy" seeds (250), the author observed that only one had germinated after one and a half months. Future studies are needed to understand the role of wild boar in the life cycle of such a key species as *Prosopis fleuoxa* in the Monte Desert.

Regarding the effect of wild boar rooting, Cuevas et al. (2012) observed that disturbed patches were modified in physical, chemical and microbiological soil properties in a short-term (fresh disturbance) (**Table 2**). Regarding the impact on vegetation, those authors found that wild boar activity through rooting produced a decrease in plant richness and diversity, generating a negative effect on perennials such as tomillo (*Acantolippia seriphioides*), jarilla (*Larrea cuneifola*) and llaullín (*Lycium* sp.), and on annuals such as verbena (*Glandularia mendocina*), papa del quirquincho (*Heliotropium mendocinum*), malvisco (*Sphaeralcea miniata*) and llantén peludo (*Plantago patagonica*). These impacts could occur either by mechanical action when boars forage and many plants remain with their roots exposed, or by consumer action, because many of these species were found in the diet (Cuevas et al., 2012; Cuevas et al., 2013b). The only species that was favored by rooting was *Pitraea cuneato-ovata*, which is an annual native species with high water requirements that grows in waterlogged and disturbed soils (Stasi and Medero, 1983). This positive effect on *P. cuneato-ovata* establishment could be due to the change of soil properties by wild boar.

The high C/N ratio found in disturbed soils indicated that nitrogen mineralization was faster in these soils (Cuevas et al., 2012). This could be because of the high soil moisture and oxygenation (lower compaction) found in those patches, or the incorporation of litter into the soil, which was found to be lower there (Cuevas et al., 2012). It should be pointed out that the longer the time between processes of mineralization and requirements of new vegetation, the lower the efficiency of nutrient uptake and use (Abril, 2002). So when mineral nitrogen is released during periods without vegetation, it is subjected to loss by leaching or volatilization (Abril, 2002). Thus, the high contents of mineral nitrogen found in disturbed soils could be lost due to rains, leaving the soil without the nitrogen needed for future plant growth (Cuevas et al., 2012). To sum up, Cuevas et al. (2012) concluded that the physical alteration of soil due to wild boar rooting has consequences on its chemical properties. And these new soil characteristics could be responsible for a reduced plant cover and less soil bulk density, which could increase soil degradation by wind erosion. Even though this impact is at the microsite scale, disturbance by wild boars could be another factor contributing to accelerating the desertification process in the Monte Desert (Cuevas et al., 2012).

DISCUSSION AND CONCLUSIONS

Globally, invasive species have a significant effect on both economic and environmental systems (Vitousek et al., 1997). In many countries, economic losses due to biological invasions have been and continue to be in the millions (Pimentel et al., 2001). At an ecological level, the establishment of new species to new environments has led to major changes in community composition and ecosystem functioning, resulting in many cases in the disappearance of native species through predation, competition for resources, spread of diseases, alteration of genetic diversity, habitat destruction, increased soil erosion, changes in hydrology and nutrient cycles, disruption of soil regimes, among other effects (Brown, 1989; Mack and D'Antonio, 1998; Byers et al., 2002; Lockwood et al., 2007). The study of invasive species in invaded habitats is necessary not only as a good opportunity to address topics such as basic processes in ecology but also the invasion process, how ecosystems function, and to evaluate the effectiveness of population management plans (Sax et al., 2007).

In this review we could observe that although wild boar is an omnivorous species whose diet consists mainly of plant matter, it prefers items rich in energy such as bulbs and fruits of *Pitraea cuneato-ovata*, *Prosopis flexuosa*, *Araucaria araucana,* and *Butia yatay*. These resources represent immediate energy for boars. Hence their main food strategy, especially in arid and semi-arid ecosystems where the majority of plants have low nutritional value due to their high fiber contents (Noy-Meir, 1973). Extreme conditions in arid and semi-arid environments involve seasonal and spatial variation of resources (van Horne et al., 1998) which can have significant consequences on the population dynamics of species, especially in periods of scarcity (Ostfeld and Keesing, 2000). High dietary intake of carbohydrates (e.g., in the fruits mentioned above) is expected to be compensated with high intake of protein from animal matter for proper nutrition (Schley and Roper, 2003). For that reason wild boar would be increasing the consumption of animal matter in periods of fruiting when they eat more food rich in energy (Schley and Roper, 2003). This was observed in both Espinal and Monte provinces. This strategy was also observed in places where the species is native and where it is introduced (Barrett, 1978; Abaigar, 1993; Massei et al., 1996; Schley and Roper, 2003).

Regarding the Subantarctic region, future studies evaluating wild boar feeding habits, including their seasonal variation, could help us understand why this species prefers *Nothofagus* forests to other types of environments. Those forests likely offer not only shelter but also food, because others studies have shown that wild boar habitat use is a function of food availability (Barrett, 1982; Welander, 2000; Cuevas et al., 2013a). Similar information on diet and habitat use of wild boar is also needed in the Pampean grassland province, where niche interactions and possible competition between this species and Pampas deer require evaluation.

The mesquite *Prosopis* spp. plays an important role in the organization of animal and plant communities (Mares et al., 1977). In Monte Desert, wild boar consume *Prosopis flexuosa*, a key species for its provision of shelter, shadow, and fruit to many native animals such as the zorro gris or South American gray fox (*Lycalopex griseus*), mara or patagonian hare (*Dolichotis patagonum*), vizcacha or plains vizcacha (*Lagostomus maximus*), and domestic animals such as cows and horses (Campos and Ojeda, 1997). In another study, Lynes and Campbell (2000) reported that 70% of seeds of American carob (*Prosopis pallida*) in the feces of wild boar germinated. Future studies on the viability and germination of seeds of *Prosopis flexuosa* in feces of wild boar are thus needed to understand the role of boars in the recruitment of this key tree species in Monte Desert.

In addition, the impact of wild boar upon Yatay palm requires additional investigation. Boars may serve dual roles as possible seed dispersers (they defecate whole seeds upon eating its fruit) and as predators upon Yatay seedlings, where during non-masting periods they dig around the plant, leaving their roots exposed and causing it to die (Ballari, 2013). Therefore, wild boar may in fact reduce the recruitment of Yatay palm in EPNP. Future studies about its role in the predation or dispersal of Yatay palm are crucial to determine this.

Regarding the impact of wild boar rooting behavior, we found evidence suggesting no substantial changes in soil properties in the Subantarctic region, whereas in the Monte Desert there were modifications of physical, chemical, and microbiological properties caused by rooting, and leading to wind erosion of soil. These differences in the impact of rooting may be tied to soil characteristics and resilience. While soils of Patagonian forest are derived from volcanic ashes with high capacity of stabilizing soil organic matter, buffering pH, and retaining P and water which confers high resistance to nutrient loss (Diehl et al., 2003), soils in Monte Desert have an inherent tendancy (fragility) to desertification attributable to an interaction between the system's own fragility due to aridity, erosive forces from water and wind, salinization processes, and anthropic actions such as livestock pressure, logging, and fire regime modification (Villagra et al., 2009). Therefore, soils in the Subantarctic region may be better buffered to short-term disturbances in comparison with Monte Desert soils, where the presence of a new disturbance factor (wild boar rooting) could have consequences such as increasing desertification.

As we mentioned above, temperature and the availability of free water are two important factors for wild boar population distribution and abundance. In several cases, when the temperature is high wild boars are restricted to areas of dense vegetation cover and close to water resources (Dexter, 1998; Acevedo et al., 2006). Cuevas et al. (2013a) observed that in the Monte Desert, daily movements of wild boars in periods or seasons of high temperature were reduced. Thus, at local scale, temperature could be a limiting factor in wild boar activity. At regional scale, wild boar could be also affected by temperature: in areas where temperature is low there is an increased presence of wild boar (Cuevas, unpublished data). Studies focused on movements, activity pattern, home range, and reproductive capacity in different climatic conditions are needed to understand why this species is so successful.

Regarding management strategies of wild boar in Argentina, Ballari et al. (2015a) found that 54% of the surveyed protected areas apply some control method. Hunting was the most commonly used technique of wild boar control, a method that managers of protected areas (e.g., EPNP, Islas de Santa Fe National Park, Laguna de Llancanelo Natural Wildlife Reserve and Campos del Tuyú National Park) have reported to be effective for reducing the boar population. However, the authors found that hunting and in combination with others methods—such as traps—were actually ineffective and did not reduce the abundance of this invasive species. In EPNP, the method of baiting the species with supplemental feeding (corn) could in fact have the unintended consequence that boars more frequently use the protected area, rather than the private agricultural lands that surround the park, due to the supplemental food being available the whole year. A similar situation was found in Europe, where landowners bait the wild boar to keep them in woodland areas and protect their crops (Cellina, 2008). While the current baiting strategy in EPNP benefits landowners, it appears to be detrimental to the park's objectives regarding the conservation of endemic species such as *Butia yatay*. Although the control method has been effective according to managers of the protected area (Ballari et al 2015a), it keeps wild boar population within the park. As was concluded by Cellina (2008) for European populations, supplemental feeding offered massively, year-round could lead to an increase in the reproductive potential of wild boars and thus contribute to an increase in their population density.

Although wild boar is recognized worldwide as an invasive species with negative effects on native flora and fauna (Lowe et al., 2000), in Argentina its management is not a priority. Its wide range in the country makes it imposible to eradicate (for logistical and economic reasons), yet it is still necessary to control it. The boar increases its geographical distribution in Argentina either by expanding its range or by the introduction of new populations for hunting (e.g. in Mendoza; Cuevas, unpublished data), or both. Thus, wild boar is still reaching new areas or localities, some of which are protected areas that involve the safeguarding of native biodiversity.

Finally, to design a management plan for wild boar, it is necessary not only to know the impact that this species generates on the environment, but also its ecological strategies in each particular area. Doing so will also allow us to better understand their potential future expansion to new areas (Simberloff et al., 2005). We conclude that the impacts of wild boar in Argentina are mostly negative, demanding interactions among different players (scientists, government officials, managers of protected areas, landownwers) to plan a strategy to control its populations, thus mitigating damage to native ecosystem and the productive systems of the country.

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